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BREEDING CHARACTERISTICS OF YELLOW-BILLED CUCKOOS IN ARIZONA

By

William J. Hamilton III and Marian E. Hamilton
*California Academy of Sciences**

The yellow-billed cuckoo is widely distributed throughout the United States, southern Canada, and northern Mexico. The nominate race, *Coccyzus a. americanus,* is found in the most suitable habitat and is one of the commonest eastern birds. There are no striking distributional gaps. Nevertheless, in eastern North America this species has received only casual attention and the only account of its life history consists of various remnant materials gathered by Bent (1940). The western subspecies, *Coccyzus a. occidentalis,* at best a weakly defined race, is more scattered, occurring only in certain relatively humid regions in the West, especially along river bottoms in the southerly parts of its range. In California some of the habits of this race have been reported by Shelton (1911) who described a population nesting along a slough in Sonoma County in northern California, and Jay (1911) and Hanna (1937) who reported characteristics of populations in Los Angeles and Riverside counties in southern California.

In Arizona the only accounts are Bendire's (1895) report of a number of nests along Rillito Creek near Tucson, and Brandt's (1951) comments on the status of the species in the San Pedro Valley near Hereford.

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* Present address, University of California, Davis, California.

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Local Environment

The observations upon which this account are based were made along the San Pedro River, Cochise County, Arizona, 4 miles downstream from Fairbank, Arizona (31°43′ N., 110°11′ W.) at an elevation of 4,100 feet, and along Sonoita Creek, Santa Cruz County, Arizona, southwest of Patagonia, Arizona (31°33′ N., 110°45′ W.) at 3,800 feet. A brief visit was made to the Patagonia area in mid-June, 1963, and an intensive investigation was made during the first 3 weeks of August, 1963, at both localities.

Brief additional observations were made at the Arizona–California border in mid-June, 1964, near Laguna Dam on the Colorado River.

Physical environment. These two Arizona locations were of considerably different physiognomy. At Patagonia a small stream, Sonoita Creek, cuts through a narrow mountain valley. On either side of the river bottom, never more than a half-mile wide and eventually narrowing to a gorge, rocky outcrops and steep slopes give way to the arid jagged terrain of the Santa Rita and Patagonia mountains. Sonoita Creek floods with seasonal rain, but the underlying rock basin forces water to the surface to maintain a permanent water flow beginning about 2 miles below Patagonia. Upstream the flow is subterranean except during the rainy season, and it is emergent only for a few hours after storms.

The San Pedro River has, by contrast, a broad river bottom, in some places over a mile wide. It centers in a sloping valley many miles wide. The drainage, from a considerable area, maintains a permanent flow. During the rainy season the shallow sandy river is over 100 feet wide in places.

These two areas, approximately 50 miles apart, share a similar climate. By late June or early July thunderstorms originating in the nearby mountains sweep across the intermountain plains, creating intermittent flood conditions in streambeds. The rivers often rise under sunny skies, the result of runoff from heavy rainfall elsewhere in the watershed. In consequence the summer climate during the yellow-billed cuckoo's stay is regularly quite humid. Only a few yards away from the river, however, the terrain becomes very dry, and the humidity drops sharply shortly after a storm passes.

Biological environment. No attempt is made here to describe the faunal of these two localities. Swarth (1929) has surveyed the vertebrate fauna of the Patagonia area.

Broad-topped tall cottonwoods (*Populus fremontii*) line the stream edge and scatter across the stream bottom of Sonoita Creek. Tree willows (*Salix*

gooddingii) edge the creek and their roots, together with occasional large rock outcroppings, fix the stream meander. Additional willows occur irregularly in the stream bottom and along lateral tributaries of sufficient drainage. These willows often rise from several main trunks and may be as tall as 40 feet. Under the cottonwoods is a ragged cattle-grazed understory of elderberries (*Sambucus glauca*), walnuts (*Juglans major*), and mulberries (*Morus microphylla*). In gravelly bars in the actual river bottom, arrowwood (*Celtis reticulata*) occurs in dense stands, a favored nesting place of the yellow-breasted chat (*Icteria virens*). Four miles below Patagonia the river bottom widens, and in this flat the ash (*Fraxinus pennsylvanica*) is exceeded in abundance only by the tree willows. At the edge of this creek mesquite (*Prosopis juliflora*) flourishes, shaded in places by tall cottonwoods. As mesquite extends from the river bottom, individual bushes are smaller and more widely scattered. They extend, however, well up on the rocky slopes before giving way to mesic vegetation such as ocotillo, century plant (*Agave* sp.), and *Opuntia*.

The woody vegetation along the San Pedro River resembles that at Patagonia. Cottonwoods, tree willow, and mesquite occupy comparable habitats. However, in the broad river bottom the Eurasian tamarisk (*Tamarix pentandra*), absent at Sonoita Creek, is a prominent feature of the broad river plain. The *Juglans, Sambucus, Morus, Celtis,* and *Fraxinus* species, so characteristic of the Sonoita Creek locality, were not found on the San Pedro below Fairbank.

One of the most important floral features of both areas was *Condalia lycioides,* a spiny shrub scattered amongst the understory of the often continuous stands of mesquite and spottily but regularly distributed amongst the river bottom vegetation. A caterpillar hosted by this plant was an important food of the yellow-billed cuckoo at both study areas in the summer of 1963.

Demeanor and Hunting Behavior

Cuckoos observed during the breeding season in August were not as vocal as most breeding songbirds. Possibly these birds become more vocal with the onset of July rains. In June they were practically silent. At that time we each spent over 30 daylight hours encamped and actively searching an area occupied by cuckoos. Yet we each heard but a single "kowlp" call. A 4-mile stretch of creek bottom was covered, listening carefully for 20- to 30-minute periods, without hearing a cuckoo. But when we played a recorded yellow-billed cuckoo call, we were at once able to locate an adult bird which had apparently been lurking nearby. Subsequent use of this technique produced two additional birds in less than 2 hours in the same area that had been so carefully worked earlier. These observations point out the inadequacy of attempting to determine presence or absence, much less abundance at this season, by observation or listening-post techniques. A more casual observer,

spending 3 hours in the field in a morning, could expect to hear less than one call a week at this season and in this area.

Skulkiness. During the course of the fieldwork in August, it gradually occurred to us that cuckoos were deliberately avoiding movement in our presence, especially nesting individuals. Continued observation confirmed this matter. When foraging undisturbed by the human observer, cuckoos would move about in the willow and ash vegetation with no apparent predilection to any particular level. High posts in cottonwoods were largely avoided. But when a bird was surprised or approached incautiously, it often retreated to a high post in the leafy lobes of cottonwood vegetation, holding this post for a remarkable period of time without additional movement. On some occasions the initial flight would take the cuckoo into the deep willow or mesquite understory, especially in areas lacking cottonwoods.

The positioning of these skulky birds was usually the same, backside to the observer. The back was arched, the body held low, the head turned slightly, watching the intruder. This performance, with the cryptically colored back oriented to the witness, the white front shaded, was a regular response to the observer. Once a bird in a willow was circled and during the periods when this bird was in view, its position relative to the observer was the same.

During these occasions when the human intruder was holding the attention of the cuckoos, they would not feed but simply devoted their time to watching and to evasive retreat. Only after repeated association with a bird, or in areas such as much used picnic grounds, would the cuckoo ignore the observer to carry out more routine activities.

Hunting behavior. Occasionally we were able to follow a bird without apparently disrupting its normal feeding routine for 2 hours or more. At first impression these birds seemed to have time to spare, being mainly concerned with scratching the head or other minor comfort movements, with much leisure time left over. For nonincubating birds this may indeed have been the case. However, it soon became apparent that what we were witnessing was the hunting mode of this bird. They are, in fact, no less alert to potential food reserves than a sparrow hawk sitting quietly on a wire over a field. Many of the actions of the hunting cuckoo are indeed quite hawklike. Much time is spent quietly waiting for the prey to reveal itself by movement.

Such a preying stratagem is suited only to predation upon large items, *i.e.*, items with a unit intake value approximately equivalent to the amount of food which could be obtained by active search in an equivalent amount of time minus the extra energy required for active versus passive prey search. The items taken were indeed quite large, consisting, so far as we could indentify them, of large moth larvae and katydids. Apparently numerous smaller insects, many perhaps belonging to the same groups as those of the larger prey items selected, were being ignored.

An account of the relatively slow feeding tempo of a hunting cuckoo on August 6 for 35 foraging minutes, spoken to a tape recorder, was as follows:

(1) At 0943 it hopped through a tree willow at the 15-foot level, then

(2) flew 60 feet to another tree willow 20 feet up, changed its perch three times,

(3) flew 40 feet to another tree willow, 10 inches from the outer limbs, and 20 feet up, took a new perch 10 feet higher in the same tree, again changed perches at this level, capered along a bare limb with tail cocked, stopped at this spot, then moved 5 feet across the open heart of the tree, to take a new post,

(4) flew across an opening to an ash, 18 feet up, and almost at once

(5) flew on 100 feet to the outer limbs of a cottonwood 45 feet up, moved 30 feet across the crown to a new post in the same tree, gave a "kowlp" call, and disappeared at 1018.

It thus changed posts 13 times in 35 minutes, with the feeding circuit including five trees, one of them only momentarily. No prey was taken during this period.

Vocalizations

"Kowlp" calls and spatial relationships. This characteristic call is the species identification tag, often the field observer's only indication of the presence of this species. It has been variously described as "an uncouth guttural sound or note, resembling the syllables *kowe, kowe, kowe, kowe, kowe!* beginning slowly, but ending so rapidly, that the notes seem to run into each other, and *vice versa*. . . " (Wilson and Bonaparte, 1878), and as resembling a rapid pulling of corks from a bottle (Hanna, 1937). We have already mentioned the almost complete absence of this or any other call by cuckoos at Patagonia in June prior to the actual breeding season. In August these calls were considerably more prevalent.

On several occasions "kowlp" calls were answered by "kowlp" calls from other individuals. In these instances when the calling bird was observed, it faced toward the other calling individual and sometimes flew off in the direction of it.

Each pair clearly ranged over several acres and it was impossible to follow any individual long enough to effectively determine its spatial relationship to its neighbors. The response to recorded calls varied from individual to individual. The observer with the recorder was approached only occasionally. Then the bird moved in with a swooping flight, tail and wings spread, and flight slowed as the bird moved past the observer and instrument to a distance beyond. Frequently the responding bird either called back at the recording or simply moved into the vicinity of the playback device, remaining silent and perched at a high lookout post.

On August 11 at 1610 a cuckoo was heard giving repeated "knocker" calls (see below) at the mouth of a dry gulch entering the San Pedro River. This bird was perched in the top of a 40-foot willow on the bank of the San Pedro. Moments later another cuckoo flew into the adjoining willow only 15 yards

from the bird giving the "knocking" call. Shortly the original bird again gave the "knocker" call. Almost at once the second bird gave a full "kowlp" call, then flew over and supplanted the original bird, almost landing on top of him. During the supplanting performance there was no obvious plumage or postural display. The supplanted bird flew off downstream. The supplanting bird found a small prey item near the top of this tree where the original bird had been, secured it, and ate it almost at once. This individual was followed as it hunted in the treetops here for the next 28 minutes. During this time it gave one additional "kowlp" call at 1635. At 1640 it flew 75 yards upstream, to within 40 yards of its nest, giving a full "kowlp" call as it landed. This and other similar field observations suggest that the "kowlp" call is associated with the species spacing mechanism.

Since birds had probably been on these areas for 2 months, it is perhaps not surprising that no clear territorial situation was determinable. If territoriality is characteristic of this species, the wide range of each pair, covering many acres, and their secretive and elusive habits will make the description of the spatial characteristics of pairs a formidable task.

On numerous occasions birds gave "kowlp" calls after a flight, immediately upon landing. On August 7 below Patagonia, at 0901, we heard a complete "kowlp" call. It was possible to visually surround the tree from which this bird called as we approached. Presently, the bird flew out of this willow, directly overhead, with labored wingbeat and in full song. This vocalization approximated the usual "kowlp" call, but the delivery was more deliberate. While it was not the typical two-parted "kowlp" call, it was obviously composed of the same notes. On no other occasion did I hear this peculiar assemblage of notes. This bird landed within sight high in a cottonwood, went through a considerable series of preening movements, and hopped to a high open perch and at once gave a full and more characteristic "kowlp" call.

On all occasions when a bird was observed giving a "kowlp" call, there was never any indication of an extension of the chest or throat.

During August we heard over 200 "kowlp" calls. Since none was ever heard beyond 150–200 yards, this was the carrying limit of this call to our ears. "Kowlp" calls were given most frequently in the early morning hours before 0700. However, additional calls were given from time to time throughout the day.

It is possible that the "kowlp" call may have a mating function as well. On June 17, 1964, along the Colorado River, what was probably a male cuckoo flew into a willow tree directly over our heads, 40 minutes before sunset. Moments later he flew to an upper position in the tree willows 50 meters from the river and gave two complete "kowlp" songs. A female joined him in the dense upper branches of this willow tree. This female took what seemed to be the preflight intention movement (fig. 1c), but exaggerated, so that her tail pointed

straight up. The male flew down, hovered over her with legs dangling, landed on her back, and either attempted to or did mate with her. This all took place quite quickly and the male at once flew off. The female remained in the vicinity for awhile, then flew off in a different direction. Some minutes later the male gave the "kowlp" call again, and was apparently rejoined by the female.

At this season (June 17–18) along the Colorado it was apparent that nesting was not yet under way, for we saw several pairs moving about *as a pair,* often separated by 50 meters or more, but occasionally coming together. Territorial boundaries seemed to be in a state of flux, but with the general spatial features already established. The frequent songs ("kowlp" calls) suggested that this population was at a stage approaching that of the southern Arizona populations we had observed on August 1 the year before. One pair was frequently observed in a tree willow overhanging the river, a site to which they repeatedly returned. Perhaps this was the potential nest site, but on June 18 there was no trace of a nest in this dense vegetation.

On these occasions when two birds were under observation for a considerable period of time only one bird of the pair was ever noted to give the "kowlp" call. It seems probable, therefore, that the "kowlp" call is limited to the male.

The loudness and ringing character of this call is probably adapted to the large territory size of this species. Little attention seems to have been paid to the volume characteristics of territorial proclamation. Increased volume should be characteristic of sizable territories, the natural sound environment playing a modifying role. This may be one reason why early morning song is so characteristic, for it is a time of environmental stillness, generally windless. Selection for lowered volume in territorial proclamation calls would come from factors of energy conservation and reduction in the number of territorial boundary encounters.

At the Colorado River area this call seemed much more variable than in the Patagonia or San Pedro areas. Here this call was often not as prolonged and sometimes terminated with but a single or two or three ringing notes. Since this population was decidedly more dense, it is possible that the more varied vocal repertoire was related to this aspect of the population.

"KNOCKER" CALL. This call, a harsh rattled call, was quite different in character from the clear "kowlp" call. Often repeated once initiated, this call consists of a series of notes blended together; each quickly follows the other to form an integrated call which sounds somewhat like a mechanical door knocker allowed to drop freely against a striker plate. Unlike the "kowlp" call, this call appeared to be limited to social situations; when we heard it we could be sure that the mate was nearby. The volume was considerably less than for the "kowlp" call and we rarely were able to hear it beyond 40 meters. A very variable call, it seemed less ritualized than the "kowlp" call, yet it was usually quite identifiable as this particular vocalization. This call is given by both mem-

bers of the pair, often several calls to the sequence, again in contrast to the "kowlp" call which was seldom repeated as frequently as once every 10 minutes. The communicatory significance of this call was never well understood by us, but the most frequent response of a bird hearing it was to return the call and fly off in the direction of it if it were not already in the presence of the mate. In close proximity return calls were regularly given. Yet we should not create the impression that these birds chatter back and forth with this call in the normal course of activity. Normally they are silent. Occasionally they give the "kowlp" call, and when disturbed or in other unidentified special circumstances the members of a pair may vocalize with a "knocker" call.

"Coo" CALL. On several occasions during August a soft many-noted cooing call was heard. These resonant sequences of cooing were repeated several times per minute, often for an hour or more. Cooing birds held high to the treetops, usually at exposed posts in dead snags 40 feet or more above the ground. Sometimes these cooing birds would range widely to the surrounding slopes several hundred yards from the river bottom, taking posts on bare oak limbs. All the while these individuals were incredibly exposed by comparison with the usually secretive demeanor of the birds in the river bottom. Moreover they did not attempt to shelter the white breast, which was sometimes visible 100 yards or more in the slanting morning light. Exposure was indeed typical of this behavior, and cooing birds moved openly along the river bottom, venturing freely into areas occupied by other birds. Occasionally other cuckoos would approach, to give the "kowlp" call once or twice, then back off. These cooing performances were persistent, with activity located in certain broad areas for days. We saw this performance from only three birds, out of a total population of more than 30 taken under observation. One possible explanation, based upon the persistence of the behavior, the response of other birds, the openness suggesting advertisement, and the visual component described below, is that this display is a function of unmated males.

Accompanying this call, with every note of each series of coos, the gular area is remarkably inflated, filling to about the size and shape of a golf ball (fig. 1). The sac is inflated and collapsed with each note. The bill is not opened, but the head falls lower and lower with each successive coo.

The number of cooing notes per sequence varied from individual to individual. A typical observation was as follows: "During the past 28 minutes, starting at 0903 (August 7, 1963) the bird has given 4 to 6 series of these coo notes per minute. The number of notes in each series does not vary to any great extent. The following count is the total notes per series for a sample run: 7, 9, 8, 6, 8, 10, 9, 11, 9, 7, 5, 9, 9, 7, 6, 6." Each sequence takes from 3 to 7 seconds to deliver and the pause between sequences was from 7 to 10 seconds.

In June of 1964 along the Colorado River we heard this call repeatedly, coming from at least three different birds. At that time the birds in that area

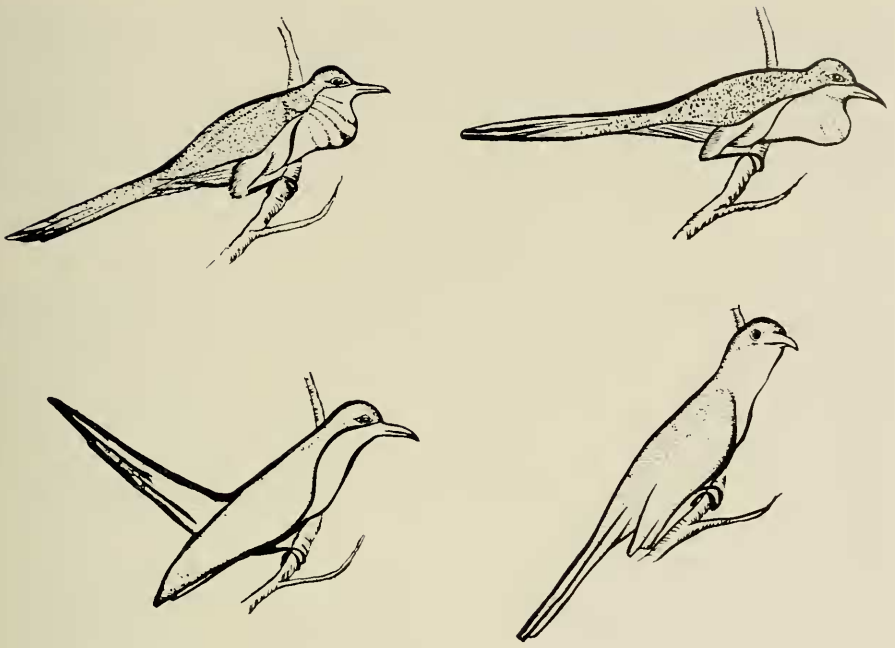

Figure 1. Postures of the yellow-billed cuckoo. The upper left shows a "coo"-calling cuckoo with throat sac inflated, the upper right the same bird at the end of a series of "coo" notes. The lower left is the flight intention movement (but see text) and the lower right is a hunting and alert (to man) posture. Drawings by Bob L. Olson.

moved about in pairs, apparently defending large territories together. The observation of coition and the frequency of "kowlp" calls suggested that nesting was imminent but not yet under way. The context of these "coo" calls was less apparent in this region since we were unable to extend observations over a sufficient period to evaluate the status of individual birds. However, these observations seem to offer additional evidence that these calls are characteristic of prebreeding behavior.

Scream. On August 18 we attempted to net the birds at a nest with nestlings. In spite of the presence of a mist net near the nest, the female at once returned to brood the young and was secured in a fold in the net when it left the nest. As one of us was climbing to within about 12 feet of the netted bird, it ceased its struggles and began to scream continuous loud, harsh, rasping cries. Almost at once the male dashed through a gap in the crown, struck the net full force, and was captured. This call as never heard on other occasions in the natural situation. These individuals gave this call in captivity on other occasions when attempts were made to grab them inside a cage.

"MEW" CALL. A unique mewing sound accompanied the distraction performance of these birds under certain circumstances (see Incubation, below). Like the scream, this call is reserved strictly for predation situations.

CALLS OF THE YOUNG. Some of the vocalizations of the young are described below under Development of the Young. It is interesting to note that in the young there is an additional unique vocalization which has apparently evolved in the context of potential predation.

INCUBATION

Data on the incubation period were obtained at nest 2. This nest was located on August 6, 1963, at 0904. It contained one cold egg. No bird was on or close to the nest. The egg was marked. On August 8 at 1025 a bird was on the nest incubating two eggs. The new egg was noticeably smaller and more evenly colored than the first. It was also marked. Daily visits on the following days confirmed that the clutch was complete at two eggs. On August 17 at 1045 the nest contained one egg and one freshly hatched young. The following morning at 1030 the second egg had hatched.

An approximate determination of the incubation period is possible based upon these data. Since the eggs hatched on separate days, incubation must have started on separate days, assuming the incubation period of both eggs was the same. The earliest incubation could have started would be the morning of August 6 for the first egg and August 7 for the second. It could have been a day later for both. This would make the incubation between 10 and 11 days. Perhaps the first egg was laid on August 5 and incubated during the nights of August 5–6 and August 6–7, with the second egg being laid the morning of August 7 and continuous incubation starting at that time. This would still leave the incubation period at 10 or 11 days.

With this incubation period as a basis, it is possible to fairly accurately estimate the timing of the start of the other nests. Nest 1 contained two young and one egg on August 13 at 1030. One of these young gaped freely when the nest was jiggled, the other kept its head down. Probably they had hatched on separate days, one on August 12 and one the morning of August 13. The third young had hatched when the nest was checked at 1255 on August 14. Presumably, then, the final egg was laid August 3 and the others on August 1 and July 29, if laying on separate days is assumed.

Nest 3 had one egg and one young when it was discovered on August 12. This egg never hatched. The eyes of the young bird opened the following day, which would make it about 3 days old when first discovered, putting hatching at August 9 and the incubation start at July 30 for this egg.

It is revealing to review historical statements concerning the incubation period of the cuckoo. The duration is currently quoted in most references as 14 days for both the yellow-billed and black-billed cuckoos. This erroneous

figure has been repeated in scores of state bird compendia and other references. The first reference to the incubation period of the yellow-billed cuckoo was by Bendire (1895): "Incubation, I think, lasts about 14 days. . . ." This qualified statement was enlarged upon by Burns (1915) who did not cite his source but indicated that all the sources of his information were "reliable." He gave the incubation period for the yellow-billed *and* black-billed cuckoos as 14 days, without qualification. It is apparent that later workers have derived their figures from this source or from one another.

The incubation period of the black-billed cuckoo was determined in 1943 by Spencer as 11 days. It thus seems likely that the incubation period of both North American cuckoos is 10 or 11 days.

Behavior at the nest. The only persistent pattern to the incubation position was that the bird never faced the heart of the tree, but always oriented at least generally away from the trunk. The long tail poses a considerable concealment problem during incubation. Held horizontally it would hang over the side of the nest, and often it is held in such a position. On other occasions the bird aligned the tail along the nest limb, but this apparently does not exceed chance. This was true at both nest 1 and nest 2. The posture of the bird at nest 2 differed from nest 1. The incubating bird at nest 2 would often sit with the tail cocked at a 45° angle with the neck and bill pointing up at the same angle. Perhaps this was simply an alert position induced by close approach to this low nest.

Incubating birds did not sit especially close. On August 10 we raised a pole with a mirror to the 32-foot-high nest 1. The bird, sitting on well-incubated eggs, flushed when the pole was 2 feet away. At this same nest on August 14, with three newly hatched young, the adult bird did not flush when one of us climbed to within 5 feet of the nest. Instead, it stood at the edge of the nest, back to the hot midday sun, wings spread, sheltering the nest. It made no move to depart until a gesture was made to approach closer. At the more strongly supported nest 2 no such approach was tolerated at any stage of the nesting cycle.

Shading the young was noted again on August 13 at 1400. The day was hot and this crown nest was shaded from the sun only by a thin sprig of willow leaves. The heat was intense. An adult stood at the edge of this nest, back to the sun, wings cupped and partially spread, but flew off when the nest was approached to within 15 feet. By the time the nest was reached, the unprotected young, pinfeathered bird was panting, mouth continuously open.

Distraction elements. A distraction display was noted at nest 1 on August 10 when we put off an incubating bird. When the bird flushed it dropped through the open undercanopy of the tree willow in which the nest was located. The wings were held high over the back, sharply cocked at the carpal joint, and opened, so that the copper red of the primaries and secondaries flashed. It

alighted first on a heavy trunk in the upper canopy 18 feet from the ground, then immediately continued its downward flutter, landing again on the trunk of the adjacent tree willow, now with the wings held more fully to the side. The tail was half fanned, the dorsal aspect oriented towards us. This away-facing posture was held, so that we could view the upper side of the wings and the dorsal side of the tail. The entire effect was one of a greater show of the coppery-red plumage in the wings than could have been presented in any other manner. The limb on which it now perched was nearly on the ground. It cocked its head towards us, then moved off into the deeper streamside vegetation. A few moments later we heard a modified "kowlp" call less than 50 yards away. On other occasions these same birds remained in the adjacent trees giving repeated "knocker" calls.

On August 16 the distraction attempts at nest 1 were more vigorous. The bird dropped almost vertically through the upper stay of the host willow's vegetation, all the while holding the wings forward and fanned. The tail was spread wide, and for the first time the bird gave an audible sound to accompany the performance, a whining "mew" interspersed with "knocker" calls. Now the mate appeared, flashing its wings. This second bird gave a modified "kowlp" call. On subsequent visits this mewing call always accompanied the distraction display.

The birds at nest 2 never performed this sort of distraction. On August 8 the bird flew directly away in a wavering flight when flushed, only 2 or 3 feet from the ground. The following day it left when we were 12 yards away. As it departed it dropped low, remaining no more than 3½ feet above the level clear ground under the mesquite canopy. The flight was slightly erratic, the tail flashed considerable white, and the red in the wings was more noticeable than in ordinary flight. On this and other occasions the departure flight was slowed. Once, a bird leaving this nest actually soared for 8 or 10 feet in much the manner and posture of a sailing nighthawk. On other occasions the wingbeat was deliberate, the deep strokes could easily be counted, and at least once were alternate.

At nest 3 the performance closely resembled that at nest 1. Like nest 1 this nest was in the crown of a sizable tree willow. These birds displayed with the wings and tail, and were very vocal with "knocker" and occasionally "kowlp" calls. On August 12, while we were examining their young, one of the birds flew from perch to perch in the nearby trees giving repeated "knocker" calls at approximately 10-second intervals.

Distraction seems, therefore, to be adjusted to the environmental situation. Under the closed canopy of the nest tree at nest 1, a slowed flight directly away from the nest would have been meaningless to a ground-traveling predator. At nest 2 this might have induced pursuit.

The distraction elements noted were, then: (1) display of bright plumage

features, including the coppery red of the wings and the white in the tail, (2) sound production, including a special mewing call heard only in this context, frequent "knocker" calls, and occasional "kowlp" calls, and (3) slowed locomotion away from the nest.

The distraction elements noted may be broadly categorized as auditory and visual. Auditory distraction was noted where a close canopy limited the opportunity for effective visual displays.

The *visual distraction* display includes the following elements: (1) the distracting bird drops almost vertically from the nest position, (2) it moves away from the vicinity of the nest at the same time, (3) spreading the wings and tail, and (4) accompanying this visual performance with a mewing call.

During *auditory distraction* this mewing call is not utilized. Instead, the bird may (1) emit "knocker" calls at intervals much more frequently than would ordinarily be produced, along with (2) a similarly accelerated pace of "kowlp" calls, while (3) circling the potential predator out of sight, but not moving away.

While yellow-billed cuckoos in most areas nest in fairly deep vegetation, they are often at the edge of openings. This is particularly true of western yellow-billed cuckoos which may nest in deep riparian vegetation, but are often close enough to openings over watercourses to permit an injury-feigning arena. In the case of the nests reported here, this adaptability to the particular local situation was prominent. In the case of nests 1 and 3, which were in deep-willow vegetation, the response tended toward auditory distraction. Nest 2, in a comparatively open area, lacked auditory distraction altogether. At nest 1 the open understory of the tree was the visual distraction arena. This again emphasizes the latitude of the response in closely adapting to the immediate situation. The distraction at this site could not be elicited simply by open space and a clear view ahead: the tree canopy precluded this visual stimulus.

Development of the Young

Abbreviated incubation is followed by a similarly rapid nestling development. The eyes open 3 days after hatching. On the 6th or 7th day the feather sheaths are methodically pulled off by the nestlings and the whole appearance of the bird changes from a quilled, dark-skinned lump, to a feathered bird with brown back and white breast. The tail is still stumpy and takes several days to grow out, but after the 8th day these birds can easily move away from the nest and, if forced, will fly to another perch. They are not easily caught.

Sound production. By the time the young are a day old they begin to make a persistent buzzing call which remains in the vocal repertoire until fledging. This call becomes louder during the 2nd and 3rd days, but thereafter its intensity no longer increases noticeably. Basically a series of very closely

spaced clicks, these calls follow one upon the other. When there is more than one bird in the nest the effect is a continuous insect-like buzz.

In captive young this buzzing is continuous during agitation. With artifical brooding, *i.e.*, a warm covering, the buzzing becomes less frequent and each burst is less prolonged, until the sound fades away. This sound accompanies begging. Nevertheless, it is not necessarily an amplification of the begging response, since it is also continued when the young are satiated and not begging. Nestling black-billed cuckoos from Ithaca, New York, made a very similar sound, but louder and crisper. There we thought this sound resembled and perhaps mimicked the solitary paper wasps which make a similar buzz before exiting their homes. The sound is well adapted to predation situations, since it is continuous, permitting few location cues, and is faint, audible at only 4 or 5 feet.

PREDATOR RESPONSES. In their first days the young show no awareness of potential predation by a human intruder. When the eyes open this at once changes. On August 16 the two older young at nest 1, now aged 4 and 5 days, hunched down when we appeared a yard away. Their eyes were wide open, but they remained motionless. At the same time the 2-day-old birds at this nest betrayed their silence and stillness, rising high and begging vigorously and noisily when the nest branch was disturbed. The same thing happened the following day. Lack of uniformity of action is obviously one of the prices paid for the advantage derived from asynchronous hatching.

By the time the young are a week old the alert posture of the adults, with tail up and wings down, is attempted by nestlings, and they may try to scramble away. From their 3rd day the young clutch at the lining or framing material of the nest when they are picked up and it is difficult to remove them without damaging the nest. The young at nest 3, about 7 days old on August 17, performed the wings down, tail up, posture and gave a hard rasping squawk. It was 2 feet distal to the nest on a large, deeply furrowed willow limb. When we started to pick it up, it dug its claws deeply into the fissures of the willow bark and hung on tightly with its toenails.

There was no opportunity to follow nestling development more than a day beyond the sheath-breaking stage in the field. From the fully feathered phase there is surely a considerable period of additional wing and tail feather development. At this stage the young weigh only about 20 grams, and they will reach 50 at maturity. But the spurt in 17 days from the start of incubation to freedom from the nest is one of the shortest for any bird, *precocial* or *altricial*. Predation might be a selective pressure favoring a rapid development, but there was no evidence of unusual predation factors in either area, and a more likely explanation is discussed below under Food.

Food

From June 12–16, 1963, the river bottom at Sonoita Creek was populated with cuckoos. At that season they were secretive (see Vocalizations: "kowlp" call), but the breeding population had apparently arrived. No observations on feeding behavior were made then and it was possible to evaluate only in general the availability of cuckoo food items.

In August the longer observation period and the breeding activity of cuckoos permitted direct observation of feeding behavior and an attempt was made to determine food items taken.

Food habits of cuckoos. The American cuckoo species seem to specialize on insects of fairly sizable proportion available locally in abundance. In North America at times other than the breeding season, a comparatively wide variety of insect and fruit species may be taken. Among the insect prey of the cuckoo are several species not usually selected by other insectivorous birds. For example, Audubon (1849) illustrates the yellow-billed cuckoo holding a swallowtail butterfly (*Papilio turnus*), and Dawn (1955) noted a black-billed cuckoo taking an adult monarch butterfly (*Anosia plexipus*), during the period of fall migration, then returning to attempt to capture another individual of the same species. An examination of a large series of stomachs revealed an entire tree frog in one (Beal, 1897), and Clay (1929) saw one hunt down a tree frog on the ground and swallow it. Lizards occasionally enter the dietary. Swarth (1929) found a whole lizard in a yellow-billed cuckoo stomach and we have seen one take a sizable *Sceloporus* lizard in central California. Reptiles are staple fare for many tropical cuckoos, so these observations are, perhaps, not surprising.

But by far the most regular and characteristic category of food items of cuckoos consists of caterpillars. These the cuckoo takes regardless of whether they are smooth, hairy, or spiny. In the eastern United States where massive outbreaks of certain tent-building caterpillars are periodic, it has frequently been suggested that cuckoos are especially abundant during these irruptions (Clay, 1929; Forbush, 1927; many others). Presumably cuckoos are recruited to areas of high caterpillar density during outbreaks such as these, suggesting a relatively nomadic phase during the period of spring arrival. In western river bottoms there may be a similar dependence upon a small number of caterpillar species during the breeding season.

Food in southern California. Cottonwood and willow bottoms along permanent freshwater courses are the habitat of the yellow-billed cuckoo in southern California (Jay, 1911; Hanna, 1937). Along the Santa Ana River and its tributaries near Riverside, Hanna (1937) found 30 nests over a period of years, with egg dates extending from May 29 to July 10.

During the first 11 days of June, 1963, we intensively worked the river-bottom areas along this river in the area where Hanna had been so successful in locating nests. Eugene Cardiff (personal communication) had heard cuckoos

in this area in recent years. But in 1963 we were unable to locate a cuckoo. Available habitat for cuckoos along the Santa Ana River has been greatly reduced owing to increasing urbanization and water-use changes. However, considerable stretches of seemingly favorable habitat remain, and most of the associated species mentioned by Hanna (*op. cit.*) are still to be found. Since the cuckoo is notably erratic in local abundance, no firm conclusions concerning its status here can be made. During this period of field investigation we were struck by the abundance of a spiny caterpillar (*Hemileuca* sp.). This caterpillar reaches a length of approximately 40 mm. before descending to the ground to pupate. In its early stages of development it is colonial and obvious. It feeds upon the cottonwood (*Populus* sp.), and several species of willow (*Salix* sp.) which flourish along the permanent sections of this stream. During June these caterpillars mature. The last instar is solitary and the coloration becomes lighter, making them comparatively cryptically colored. It seems possible that the June and July breeding season of the cuckoo, so clearly established by Hanna's large series of nests, may be timed to this caterpillar species here. Most other species in this area, insectivorous and seed eating, complete their breeding cycle considerably earlier.

Nests

The three Arizona nests upon which this account is based were examined entire, then turned upside down and taken apart. Since there was practically no intertwining of components, nests came apart piece by piece in about the order of original construction. While these nests were basically similar to those described above and to one another, several differences indicate a certain versatility adapted to the nest site and to available materials.

Anchoring. Versatile adaptation of the nest to its site was well illustrated by nest 3. This nest was centered in the uppermost and outermost branches of a 35-foot tree willow at the fork of a 1-inch branch. The first material laid down was a series of 51 dead willow twiglets close to the fork. The nest was not centered over this start, however, but was 65 mm. more distal. It seems that in order to properly secure the nest this preliminary anchor was constructed. By comparison, the anchoring and framing materials of nest 2 were indistinguishable. This nest was also placed in a fork, but the broader branches were larger and the nest was nearly centered over the fork. The anchoring material of nest 1 could not be examined. In removing it from its treetop position 32 feet over a stream this material pulled away.

The anchoring branchlets and the framing materials of all nests were all either mesquite or willow twiglets except for one tamarisk branchlet in nest 3. In nest 3 the first 51 twiglets were measured (table 1). The uniform diameter and fairly uniform length of these twiglets is probably not simply a reflection of the size twig which is easily broken off since there were a few which were

TABLE 1. *Consecutive measurements in millimeters of the first 50 willow twigs laid down in cuckoo nest number 3.*

No.	*Diam.*	*Len.*	*No.*	*Diam.*	*Len.*	*No.*	*Diam.*	*Len.*	*No.*	*Diam.*	*Len.*
1.	1.8	110	14.	1.9	190	27.	1.8	100	39.	3.4	110
2.	2.1	130	15.	2.5	140	28.	2.3	240	40.	2.8	100
3.	1.5	90	16.	2.3	170	29.	2.0	90	41.	2.1	170
4.	1.9	170	17.	2.1	130	30.	2.3	200	42.	2.3	90
5.	2.2	110	18.	2.4	160	31.	1.9	60	43.	2.2	130
6.	2.0	190	19.	2.1	150	32.	.8	140	44.	2.1	120
7.	2.1	110	20.	1.3	80	(Tamarisk Branch)			45.	2.5	140
8.	1.5	90	21.	1.9	120	33.	2.2	190	46.	2.6	140
9.	1.7	120	22.	2.9	180	34.	2.3	160	47.	1.8	70
10.	1.7	150	23.	1.0	50	35.	1.8	110	48.	2.4	280
11.	1.8	130	24.	1.9	100	36.	1.9	150	49.	1.5	90
12.	1.8	110	25.	2.0	100	37.	2.7	270	50.	1.9	70
13.	2.1	100	26.	2.2	160	38.	2.5	270	51.	1.8	180

considerably larger. In Ohio, Clay (1929) observed a yellow-billed cuckoo breaking off twigs for nesting material with the bill.

These anchoring branchlets are laid across one another in a random pattern, some extending well to the side of the main nest as supporting outrigging extending over the hosting limbs. All of the branchlets used in nest 3 were terminal tips. The majority were placed with the butt end outward. The outermost anchoring branchlets and the outermost framing pieces above them which did not cross under the center of the nest were the longest. Several of these long branchlets were curved, the contour of the curve forming the outline of the nest.

When I attempted to make a similar structure I had considerable difficulty at the start in keeping it from dropping through the crotch of the nest site. This was a lesser problem if branched twiglets were used, and the most complete nest, number 3, was examined with this in mind. Of the 51 twiglets listed in table 1, 9 of the first 10, 6 of the second 10, and 5 of the third and fourth 10's, and 4 of the final 10, were branched. Branch 32, of a different material, was not included in this tally. Evidently cuckoos resolved the problem of having the initial structure collapse some time ago, and tend to use branched twiglets when starting their nest.

The first item laid down in nest 1 was a bunch of three 90-mm. willow leaves. This nest, unlike nests 2 and 3, was placed on the top of a limb. A leafy start would, of course, only be possible at such a site. Above these three willow leaves were four cottonwood leaves, then a nest frame of willow branchlets much like nest 3. These leaves appear to have come from the tents of a hairy caterpillar whiched flourished in the river-bottom cottonwoods during June, 1963. These communal caterpillars, under the protection of web tents, eat both sides

of the surface flesh of cottonwood leaves, leaving the vein structure of the leaf intact. It was four of these leaves that followed the willow leaves into nest 1. Their presence in this nest confirms the presence of cuckoos about these tents. It may also suggest that actual nest construction was initiated, at least in a preliminary way, by late June or early July. They may have been placed in the nest along with the willow leaves when nest-site selection was under way and the actual process of nest construction had not yet started. However, some of these leaves persisted into August, and could have been obtained then.

FRAMING. Above the anchoring material in nest 3 there were 92 additional willow twigs. As with the anchoring pieces, the butt ends are most frequently pointed outward. These pieces are on an average shorter than the anchoring members and only a few spikes stick out from the nest to give it its pincushion appearance.

In nest 2 the anchoring material and the framing stuff were indistinguishable. In this nest these parts were all mesquite, the species of the host tree, in spite of an abundance of nearby willows. Perhaps this is more a concession to concealment than necessity. These larger branches conformed neatly to the host tree, hiding the nest much more effectively than if it had been made of willows. These twigs were of much greater diameter than the willow twigs used in nests 1 and 3. There were 137 of these mesquite twigs below the lining cup.

Throughout the anchoring and framing portion of the nest, there seems to be no indication of weaving. However, the twigs do seem to be poked into place at the higher levels, and the precise order of insertion was difficult to determine.

LINING THE NEST. Above the frame the construction materials change abruptly to lining items. In nest 3 the material from the lining was about 6 mm. thick and consisted of strips of bark, leaves, and a great number of small twigs from the river cedar. A count of this latter material did not seem very useful since it was probably gathered in mouthfuls rather than as individual items. There were several hundred individual twiglets of this material and several larger much branched pieces. The whole of this material could have been gathered very quickly near the nest tree.

In addition there were 7 pieces of stripped bark in this nest, to 260 mm. in length and 15 mm. wide. The rest of these pieces were less than half as large. Two of these straps were wrapped over a framing willow twig and pushed back into the cup material. This was the only evidence of any weaving in any of the three nests examined.

Additional material in this nest included eight small separate willow leaves, a single small cottonwood leaf, and four mesquite leaves which had broken apart to a considerable extent. It seems likely that the mesquite leaves which Brandt (1951) found in his nest fell apart on drying rather than being stripped as he suggests.

The lining of nests 1 and 2 was similar but the area of these nests near Patagonia lacked the tamarisk material. We did not find this plant at Patagonia. The 6 mm. lining of nest 1 started with a flat mat of 6 willow leaves. These may have been placed fresh, since they were matted quite flat. These leaves were oriented so that the long axis of the leaves followed the long axis of the nest. Above these leaves there were additional mesquite leaves (entire compound leaf) and a number of cottonwood bark strips. These could have been obtained easily from almost any nearby cottonwood tree since almost all of these trees had a number of large dead branches with bark stripping away.

The lining of nest 2 was more than twice as deep as in the other two nests. This lining was clearly stratified. As in nest 1, broad leaves start the lining, in this case 17 caterpillar-eaten cottonwood leaves. Above these followed a mixture of broken mesquite leaves, 9 willow leaves, 11 additional pieces of mesquite twigs all about 50 mm. in length, a branchlet of ash seeds, and a small packet of unidentified capsular seeds. Finally, there was a lining of several strips of bark, more than a dozen rootlets, and two oak leaves.

All of the lining above the cottonwood leaves seems to have been added after the first egg was laid since my notes indicate that on the day the nest was discovered, August 6, it was lined with three cottonwood leaves, and it was only by the grace of these three leaves that the egg was not visible from below.

OVERALL FEATURES OF NESTS. The greatest overall dimensions of these nests were as follows: The frame of nest 1 was not measured. The cup was 102 by 275 mm. Nest 2 had a frame 275 × 360 mm. with a cup 84 × 112 mm. Nest 3 was 290 × 365 mm. and had a cup 115 × 140 mm. These dimensions emphasize the oblong and somewhat unsymmetrical appearance of the nest. From the nest cup the brooding bird overhangs the cup but only the tail exceeds the frame. The frame material effectively breaks up the outline of the bird which would otherwise, in a nest of more modest dimension, be silhouetted against the background.

BEHAVIOR OF ADULTS RELATIVE TO THE NEST. That this may indeed be a very adaptive structure is illustrated by an experience with the adults of nest 1. After the eggs hatched in this nest, the nest was shifted to a lower position in the tree in order to facilitate netting the adults at a later date. The entire nest was placed on a rimmed wooden platform slightly larger than the anchoring branchlet lengths. *The sitting bird could thus not see through the nest to the ground.* On August 16 at 1545, when I approached the tree to check the progress of the nest, a stiff wind was blowing, the promise of an oncoming thunderstorm. The major trunks of the tree, including the displaced nest, were swaying considerably. I was anxious to flush the bird so it would not be startled and perhaps injure the young. So when I reached the branching trunk 8 feet below the bird, I banged the trunk and shook it. The bird was unperturbed, and remained on the nest, with the tail hanging over the edge of the platform. It finally flushed when

I was only 4 feet below and in sight. On other occasions these birds would leave when we were over 20 feet away. The advantage of the open nature of the framing material is demonstrated by this experience. It allows a careful watch of movement below the nest and at the same time conceals the brooding bird.

Nest building. Our arrival on August 3 was probably too late to witness nest construction activity. However, on August 4 at 1545, following our 5 hours of intermittent rain, Clark Ross observed a cuckoo, probably one of the nest 1 birds, in the top of a mesquite tree along a nearby tributary creek. First it flew into a mesquite tree and gave the "kowlp" call. It then picked off a short dead leaf from a mesquite tree, dropped this item, did the same with another leaf, and finally selected a larger dead leaf and flew off with it to the base of a nearby hill. This would be in the direction of nest 1, which contained three eggs at that time, with incubation just under way. There are several possible interpretations of this observation. It is possible (1) that nest improvements continue after incubation has started, (2) that the continuing rain stimulated an attempt to dry or improve the nest lining, (3) that the nest building tendency had not completely subsided in spite of the recent completion of the nest, or (4) that the nest material gathering movements were a displacement activity resulting from some social encounter not sensed by the observer.

Incomplete nests and their interpretation. The entire lining of the nest seems to be omitted on certain occasions, while at other times it is less complete (Hanna, 1937). Since the lining phase of nest construction is a distinct step, its omission may reflect an inherited trait, perhaps favored in areas of high predation or moderate climate during incubation.

Migration

In Arizona the yellow-billed cuckoo is strictly a summer resident. The winter quarters for this population are unknown, but probably include the jungles of South America where the species winters, from Venezuela to Argentina (A.O.U. Checklist, 1957).

Spring arrival. For a bird as unobtrusive as the cuckoo, migratory schedules are best established by workers who are in the field continuously through the spring and after the breeding season. In 1927 Swarth (1929) was in the vicinity of the Patagonia study area from May 10. He first observed yellow-billed cuckoos at Patagonia on May 25 and "others were seen and heard several times during the next few days, and it seemed evident that they were just arriving from the south."

Other evidence suggests that cuckoos are on the move later than June 1, however. At Sycamore Canyon, Arizona, Miller (1950) observed what he interpreted as a migratory wave on June 30, 1945. He had been encamped at that locality 2 days before this species was observed. They were quite vocal for a day or two, then none were seen.

At some western localities these cuckoos apparently occupy upland country prior to actual breeding, invading riparian woodland only when it is time to breed. In Sonoma County, California, Shelton (1911) states that "this bird keeps to the higher land, among the oaks and other timber, for a period of two or three weeks before retiring to the willow bottoms to breed." And in southern California Baumgardt (1951) watched a yellow-billed cuckoo eating caterpillars on manzanita in the San Bernardino Mountains at 5,000 feet on June 2, 1950. This is a habitat completely different from the lowland riparian habitat occupied by the species during the breeding season. In the Cape Region of Baja California the species has been reported in the mountains in midsummer. This may be the retreat of this species prior to its arrival in lower riparian situations to breed later in the summer (Brewster, 1902). But other workers have subsequently searched these mountain areas without obtaining evidence of cuckoo breeding populations (Van Rossen, 1945).

Fall departure. Swarth (1929) continued fieldwork through the period of fall migration. He notes: "During the last week in August cuckoos were seen in fair abundance about Patagonia, and in lesser numbers somewhat later, the last on September 11." I have examined five specimens taken by his group at that time, now in the collection of the California Academy of Sciences. A specimen taken in the Huachuca Mountains, Arizona, August 31, was an adult as were two birds taken at Patagonia on September 5 and 9. Two additional specimens taken at Patagonia on August 31 and September 11 were juveniles, easily identified by the less strikingly patterned tail feathers. It would appear from this scant evidence that the adults do not precede the departure of the young by any considerable degree.

Discussion

Limiting factors, biological. The overall picture which this study produced was one of cuckoos breeding at a density considerably below that which the *apparent* food supply would permit. It is possible that food, in fact, is not a factor limiting the abundance of this species, but in Arizona we found no evidence of other environmental population-limiting mechanisms.

In considering the food supply with respect to the cuckoo population, three possibilities become evident. First is that breeding densities and spatial distribution of breeding pairs are adapted to the average or lowest year of food abundance. In 1963 the caterpillar which formed the major part of the diet of the young might have been unusually abundant. At the San Pedro River location there were, in fact, fewer caterpillars than along Sonoita Creek. Nevertheless, even there they seemed to be superabundant.

Second, what seems to be a superabundant food supply may be basically marginal to begin with. The caterpillar of the *Condalia* bush which is the main item taken to the young, is a relatively small prey item for the cuckoo, and

they are taken one at a time. Since each caterpillar it treated before feeding to the young or before being eaten by the adults, the labor involved in flying out to a *Condalia* bush, obtaining a caterpillar, and returning to the nest, would be considerable. Thus, it may be that several of the breeding adaptations of the yellow-billed cuckoo in Arizona are adaptations to time limitations with respect to this caterpillar.

A third possibility is that the spatial distribution characteristic of the yellow-billed cuckoo is adapted to other regions of quite different nutritive characteristic. There is some evidence to support the contention that gene flow from other areas is significant. The western race of the yellow-billed cuckoo is poorly defined and additional races from either Mexico or other regions have not been suggested. In other parts of North America the spatial requirement for successful breeding is probably greater. If the relatively small populations in Arizona are swamped by gene flow from these cuckoo populations, the yellow-billed cuckoos of Arizona might have no opportunity to evolve spacing mechanisms locally adapted to a particularly favorable food resource. It seems reasonable, therefore, to suggest that the density regulation mechanism of the Arizona populations may, in fact, reflect the requirements of the species population center in the eastern United States.

Limiting factors, physical. Possibly the location of nest sites is restricted to river bottoms because of humidity requirements for successful hatching and rearing of the young, regardless of the proximity of food. In the San Pedro River locality there are numerous stock ponds which have large cottonwoods and willows about them. Some of these ponds have permanent water. Near Saint David, Arizona, yellow-billed cuckoos were seen about these ponds in mid-August. While no nests were found, it seems likely that the species breeds there. Except for these ponds, no cuckoos were seen other than in the immediate vicinity of river bottoms. Along Sonoita Creek no cuckoos were noted above the region of permanent water. These observations suggest that permanent water or some environmental factor closely correlated with it are a basic requirement for the yellow-billed cuckoo. At the San Pedro River locality the *Condalia* shrub and its caterpillar extended several hundred yards beyond the river bottom. Cuckoos flew out to these areas to feed, but nests were apparently all located along the river bottom. The denser cover in the river bottom would not seem to be the sole factor dictating this choice since nest 2 at Sonoita Creek was in a mesquite tree, a few yards from the river bottom. Mesquite is the predominant shrub in the area for a considerable distance beyond the river along the San Pedro. The nest along the San Pedro River is on interesting example with respect to this hypothesis. Only 30 yards from the tree willow which supported this nest the humidity became strikingly lower. The extremely arid region adjacent to the river-bottom area was consistently less humid.

This suggestion again considers the genetic adaptation of the species as a whole throughout North America. The species population center in the eastern United States is concentrated in the deciduous forests and meadows which are consistently humid during the early summer breeding season of the species there. River bottoms in the west could be easily adapted as geographic barriers were penetrated. However, the utilization of a breeding terrain strikingly drier than that used by the species as a whole might be precluded by the lack of an adaptation permitting successful egg hatching under these conditions.

ADAPTATIONS TO SEASONAL BREEDING. Compared with most temperate region songbirds, the yellow-billed cuckoo has an exceptionally long breeding season in the eastern part of its range. In the southeast and West Indies breeding begins in April, but may be delayed until June in the northen part of the range. In the southeastern United States the species may be double brooded, but this has only been inferred from the discovery of a progression of nests not necessarily by the same individual, as the season progresses. In every part of the species range exceptionally late nests have been located. Extremes are a nest with two young on September 9 in Missouri (Adams, 1933), incubated eggs in Alabama on August 11 (Golsan and Holt, 1914), eggs as late as August 15 in New Jersey (Harlow, 1918), four eggs in a nest in Illinois on September 5 (Hess, 1910), eggs in Alabama on August 10, 11, and 14 (Holt, 1925), fresh eggs in Florida on August 11 (Williams, 1904), and eggs in Michigan on August 27 (Swales, 1903). The latest date appears to be for the black-billed cuckoo, which was found sitting on four fresh eggs on September 14 in Michigan (Barrows, 1912) and with young in New York on September 10 (Bendire, 1895). These extremes point to the fact that in the breeding range as a whole reproduction may occur almost any time the species is present. This wide range of the reproductive season suggests at least a partial role of environmental control of reproduction. In addition it suggests a preadaptation to taking advantage of an abundant food source when it becomes available at a season not in phase with the usual breeding season. In the case of the yellow-billed cuckoo, however, the range of variability of the eastern populations includes the adaptive season in Arizona, and adaptation to this area would have been possible by selection from the genetic pool of the species: no new mutations would be necessary.

The wide range of breeding seasons presents an interesting problem with respect to the basis of their timing. If we accept Lack's (1954) hypothesis that the breeding season of altricial birds is timed to the maximum abundance of food, a well-supported hypothesis in general and one which seems to be supported in the case of these several populations of cuckoos, then the regulation of the timing of the breeding season presents a particularly interesting problem for this species. Several aspects of the breeding cycle in southern Arizona and southern California are compared in figure 2. The difference in breeding season

of these two populations could be based either upon local adaptations of mechanisms which permit the initiation of egg laying in anticipation of the maximum food supply or actual timing by the appearance of a satisfactory food supply.

The tent-building caterpillars in Arizona which were present in June provide interesting evidence with respect to these alternatives. If the mere presence of a rather abundant favorable food species triggered reproduction, this comparatively small outbreak could conceivably have triggered a flurry of breeding at a very inappropriate time. Yet breeding bypasses this false opportunity. During the latter rainy season in July and August when the flush of breeding occurs, not only are caterpillars available but alternate food resources such as other caterpillar species, grasshoppers and beetles would provide at least a partial substitute should the caterpillar crop fail.

It would be reasonable to suggest that breeding was timed by the seasonal rains here only if one assumed that this timing is a local population characteristic, since the nearby southern California populations breed at a season when there is no likelihood of any rain during their breeding season. And, lacking any evidence of large-scale genetic adaptations to local environments, it seems too much to expect that behavioral characteristics would be so different in these nearby populations.

Several features of the breeding cycle point to the possibility of adaptation to exogenous regulation. In particular, the tremendously abbreviated incubation period and rapid nestling development point in this direction. However, this could be an equally effective adaptation to a genetically timed cycle which takes advantage of the food supply available for only a brief period of time. If the clutch size of the Arizona population is actually reduced, as it seems to be, this could again be construed as evidence for genetic adaptation to a sharply resticted period of adequate food supply for the young.

ADAPTATIONS OF THE SPECIES. The field observations reported here and the general ecological situation suggest several aspects of the overall adaptation of American species of cuckoos to their niche not previously discussed elsewhere. A part of these imply specialization, but in general these adaptations seem relatively broad. In comparison with other species of similar size, the yellow-billed cuckoo is usually less abundant. This probably reflects the role of the cuckoo as a predator on sizable prey species.

A major adaptation which the yellow-billed cuckoo has made is with respect to a seasonally available, and comparatively abundant, source of food which has not been fully utilized by other species. In particular, the hairy tent-building caterpillars in the eastern portion of the range and certain species of spiny caterpillars which are rejected by other species are favored food items of the cuckoo. Combined with this predilection to secure food items which are not utilized by other species is an ability to time the breeding season to local

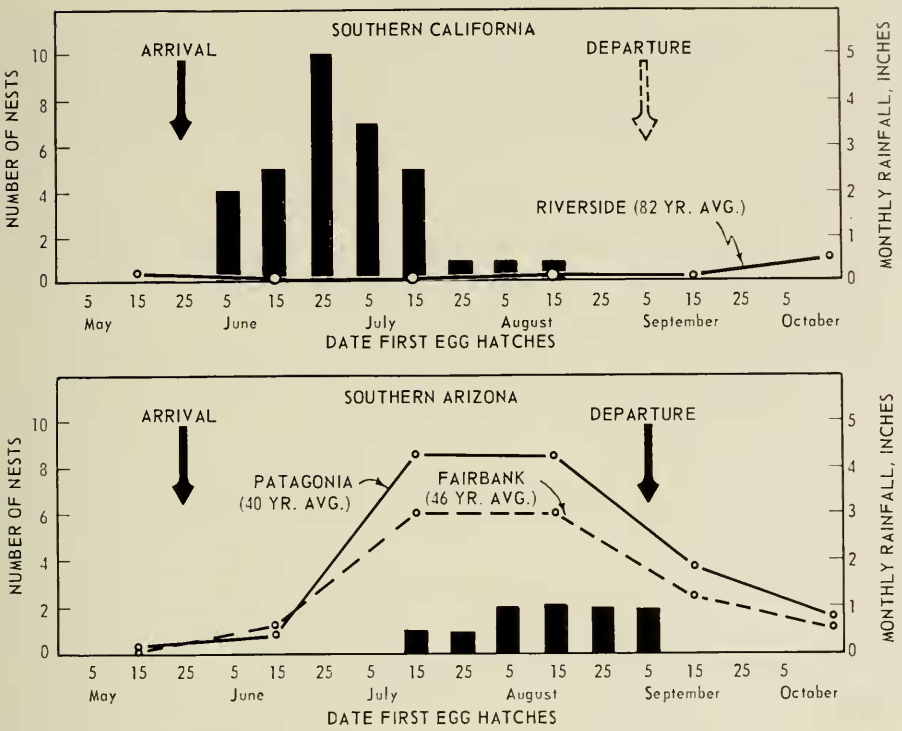

Figure 2. Breeding characteristics of yellow-billed cuckoos in southern California and southern Arizona. These dates are compiled from the literature, collections, and original observations. Five days were added to egg dates unless stage of incubation could be determined. The number of nests for southern California reflects the greater amount of study directed to cuckoos in that area. The departure dates are approximate and it is obvious that birds which hatch during the week of September 5 in Arizona can not leave that early. This discrepancy reflects inadequate data and a span of departure times; the entire population does not leave at once. Weather data are from U. S. Weather Bureau records.

conditions of food abundance. The observation of Bendire (1895) of cuckoos carrying a large number of sizable crickets (*Anabus*) to nestling young emphasizes that the yellow-billed cuckoo is adaptable, and not, at least as a species, restricted to a limited diet.

Timing of migration. In spite of the sharply different breeding seasons of the southern California and southern Arizona breeding populations, migration is accomplished by both populations at approximately the same time (fig. 2). In the case of the Arizona population this takes the species to the breeding grounds well in advance of the breeding season. There seem to be two plausible explanations for this characteristic.

First, it is possible that the time of migration of the species is adapted to

anticipate the season of maximum opportunity for the species as a whole. Since a relatively small part of the whole breeding population is breeding in a place with the late summer thunderstorm ecology of Arizona and Mexico, the fixed timetable of the vast majority of the population may swamp any tendency to adapt the migratory schedule more closely to the period of maximum food abundance.

Another possibility is that the premature arrival at the Arizona breeding locality simply reflects the necessity to vacate feeding grounds on the winter quarters which become inadequate, or at least less favorable, compared with what is available at the prebreeding Arizona environment.

INCUBATION PATTERN. Audubon (1849) was shown a yellow-billed cuckoo nest at Charlestown, South Carolina, which had two feathered young able to fly and three additional young of different sizes. In addition, the nest contained two eggs, one containing an embryo, the other fresh. None of the young were of the same size. Based upon the comments of the discoverer of the nest, Audubon felt that laying in the same nest continued over a prolonged period of time. It is now apparent, however, that the eggs of the American cuckoo species are laid in clutches. Incubation apparently begins soon after the first egg is laid. Thus, the young hatch either daily or every other day. Perhaps occasionally a longer span may separate hatching dates. This staggered incubation pattern is characteristic of owls, some hawks, coots, and a number of other species. It has often been suggested that the adaptive significance of this pattern is to insure that at least a part of the clutch receives adequate food. Thus, the first-born will, with even a minimum amount of food, be vigorous and obtain food at every nest visit by the parent. During times of food shortage the last young to hatch will be neglected and will not limit the survival potential of the first-born.

An alternative hypothesis is suggested by the limitations which seem to be imposed on cuckoos by the nature of their caterpillar food supply which they depend upon to such a great extent. If the amount of food which can be delivered to the young is restricted by time, *i.e.*, the time required to fly out, obtain a caterpillar, return to the nest, treat the caterpillar, and deliver it to the young, rather than being limited by the overall abundance of food, then a staggered hatching sequence would be of considerable advantage. This would permit a greater number of trips for those young at a stage with maximum food requirements and would extend the period of productive food gathering.

The early fledging of the young and their especially early departure from the nest are also adaptive in connection with the considerable pretreatment which each caterpillar receives before it is ingested. If the young mature to a state of being able to move to the caterpillar source and do their own food manipulation at an early stage, a considerable time economy would be achieved.

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